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Title: Influence of Leaf Types on Canopy Architecture and Grain Yield in Selected Crosses of Spring Wheat (Triticum aestivum L.)

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The effects of erect leaf canopies on enhancing grain yield in wheat is not understood. The main objective of this study was to understand the effect of leaf angle on grain yield by comparing randomly derived-lines from crosses of erect and droopy leaf spring wheats. Nine traits associated with canopy architecture were evaluated to determine their influence on grain yield and its major components. The experiment was conducted at Centro de Investigacions Agricola del Nororeste (CIANO) located near Obregon, Mexico.

When all F6 lines are considered, there were no consistent differences in grain yield between different canopy types. Parental sources of erect and droopy leaf type did, however, have an influence on the interrelationship between components of grain yield. In the highest yielding cross, F6:2 lines showed positive complementary relationships between grain yield, grains/m^2, harvest index, and 100 kernel weight. That erect leaf F6:2 lines were included in the top and lowest grain yielding groups indicates that factors other than leaf erectness may be more important in determining grain yield.

In a separate experiment, paired F6:2 lines with contrasting leaf types of crosses between erect and droopy leaf parents were derived from individual F2 plants. Erect leaf lines showed a slight grain yield advantage over their droopy leaf counterparts. The differences in grain yield were associated with high grains/m^2, high harvest index, and slower leaf senescence. Erect leaf F6:2 lines also showed a higher crop growth rate. However, the grain yield advantage in erect leaf F6:2 lines was independent of efficiency of converting solar radiation into dry matter, crop growth rate, extinction coefficient, and leaf area index.

Erect leaf parents and erect leaf F6:2 lines showed higher susceptibility to leaf tip burning. Negative associations of leaf tip burning with grain yield and its components were found among erect leaf F6:2 lines. Leaf tip burning reduced 100 kernel weight, and consequenctly yield.

The erect leaf habit in wheat may have some beneficial impact on grain yield, provided appropriate parental sources can be identified. Selection for high grains/m^2 and 100 kernel weight in erect leaf populations may maximize selection response.

INFLUENCE OF LEAF TYPES ON CANOPY ARCHITECTURE AND GRAIN YIELD IN SELECTED CROSSES OF SPRING WHEAT *Triticum aestivum* L.

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Typed by Apichart Vanavichit

In Dedication To:

Ubolratana Vanavichit, my mother

Dr. Boonrod Binson, my uncle

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INTRODUCTION

Grain yield in wheat is determined by i) dry matter production, and ii) partitioning of dry matter into grain yield. In theory, leaf angle in a wheat crop canopy might affect grain yield both by enhancing photosynthetic efficiency, and influencing the relations among components of grain yield. Upright leaves may influence photosynthetic efficiency by allowing for more light to be available to the lower leaves without reducing photosynthesis in upper leaves (Hay and Walker, 1989). Mathematical models have predicted that under conditions where leaf area index (LAI) is greater than 4, crops with erect leaves will have photosynthetic and crop growth rates higher than those with droopy leaf form (Monteith, 1965; Witt, 1965; and Duncan, 1971).

Experimental evidence that an erect leaf habit was advantageous for enhancing photosynthetic efficiency has been reported for rice *Oryza sativa* L. (Hayashi and Ito, 1962); for barley *Hordeum vulgare* L. (Gardener et al, 1964); for forage grasses (Hunt and Cooper, 1967; Cooper et al., 1970); and for sugarbeet *Beta vulgaris* L. (Watson and Witts, 1959). However, inconsistent experimental results have been reported for wheat *Triticum aestivum* L. (Puckridge and Ratsowsky, 1971; Austin et al., 1976); barley (Berdahl et al., 1972); and maize *Zea mays* L. (Moss and Musgrave, 1971; Sinclair et al., 1971). According to Loomis and Geratis (1975), the controversy is related to differences in LAI being too low to observe the positive effects of erect leaf on photosynthesis.

Whether leaf angle affects grain yield in small grains remains a matter of debate. Evidence suggesting a benefit of erect leaf on grain yield has been reported in rice (Tanaka et al., 1969; Tanaka and Matsushima, 1971; Change and Tagumpay, 1970). Yoshida (1972) indicated that leaf erectness can be used as an effective selection criterion for enhancing grain yield in rice. No consistent evidence supports the idea that leaf angle may directly affect grain yield in wheat (Austin et al., 1976; Davidson and Sayre, 1988); or in barley (Tungland et al., 1987; Angus et al., 1972).

There is some evidence that erect leaf may influence grain yield indirectly through i) tiller survival (Berhadhl et al., 1972), ii) water use efficiency (Innes and Blackwell, 1983), iii) tolerance to high plant densities (Stoskopf, 1967) in small grain, and iv) enhanced tassel-silk synchronization by reducing ear shading in maize (Lambert and Johnson, 1978).

Inconsistencies in experimental results found in the literature may be attributable to different methods for quantifying leaf erectness, to differences in LAI or to the effects of genetic background. A critical study requires near-isogenic lines different only for the contrasting traits. However, generating such experimental materials is time consuming, and the genetic background may not be suitable for the expressivity of contrasting traits (Cooper, 1975).

In this study, the specific objective of this research was to understand how leaf angle influences light interception, dry matter production, harvest index, components of grain yield, and grain yield. Two methods of generating experimental materials suitable for evaluating the effect of leaf type on grain yield were employed. Both used randomly derived lines resulting from crosses of erect and droopy leaf parents. In the first approach, F6 lines were derived at random from individual F2 plants. Progenies were then classified into two groups of leaf type--erect and droopy--based on discriminant function analyses. Comparisons were then made between and within groups for canopy architecture in relation to light interception, components of yield, harvest index, and grain yield.

In the second approach, paired F6:2 lines with contrasting leaf types were generated from individual F2 plants. Contrasting pairs were compared for canopy architecture, light interception, LAI, extinction coefficient, efficiency of converting intercepted solar radiation into dry matter, crop growth rate, components of yield, harvest index, and grain yield. The paired F6 lines generated from the same F2 plant would share nearly similar genetic background, thus providing more precise comparisons.

LITERATURE REVIEW

In breeding for grain yield per se, Evans (1983) noted that "yield potential is the result of having an adapted cultivar grown in an environment with optimum nutrients and moisture and where pests, diseases, weeds, and other stresses are effectively controlled." Under such conditions light and CO_2 are the main limiting factors. Plant breeders and physiologists are trying to improve the photosynthetic and photorespiration system through the manipulation of the plant canopy in order to enhance the partitioning of dry matter produced into grain yield.

Several investigations have studied leaf angle and its affect on photosynthetic rate. The hypothesis that erect leaf might affect grain yield was first proposed by Boysen Jensen (1932, 1949). His arguments were that i) a dense crop with erect leaves would have a higher photosynthetic rate than the one with droopy leaves, ii) since in the field most light is transmitted vertically, an erect leaf canopy would distribute light more evenly over leaves. The hypothesis was not supported by experimental data.

Models for Measuring Photosynthetic Rates

Monsi and Saeki (1953) proposed a model to predict plant productivity as a function of leaf angle, light intensity, and leaf area index (LAI). They found that the equation $\log (I/I_0) = -K \times LAI$ adequately described the relationship between LAI and light penetration, where I/I_0 is the fraction of light penetrating a layer of LAI, and K is the extinction coefficient or the slop of the curve when $\log (I/I_0)$ is plotted against LAI. In general, the extinction coefficient is lower for erect and higher for droopy leaves.

Models have been used to predict the dependence of photosynthetic rates on leaf angle under various conditions. Trenbath and Angus (1975) summarized that "all models are agreed in predicting that at LAI > four a crop with erect leaves will have higher gross photosynthetic rate per unit leaf area than droopy leaf type."

How erect leaves affect efficiency of utilizing intercepted solar radiation and influence crop growth rate was described by Hay and Walker (1989). They noted that i) upright leaves will intercept a smaller proportion of incoming radiation at high solar elevations, leading to an improvement in photosynthetic efficiency at the top layer of the canopy as the irradiance incident upon the leaf surface is reduced to the saturation point, and ii) light will become available for photosynthesis at the lower layer of the canopy.

An ideal plant canopy was proposed by Blackman (1961) where the upper leaves are increasingly angled to avoid wasteful interception of light above the saturation point. Duncan (1971) provided computer models supporting the idea that a canopy with vertical leaves near the top, and horizontal leaves towards the bottom, provides the most efficient system for dry matter accumulation.

A wheat ideotype was also proposed by Donald (1968) as a short, strong, uniculm with few erect leaves and bearing large erect spikes with awns. The ideotype was expected to perform or behave in a predictable manner within a defined environment that is non-limiting for water and nutrients and to be a weak competitor against a similar plant type in the crop community.

Effects of Leaf Angle on Photosynthetic Efficiency and Crop Growth

Watson and Witts (1959) provided the first evidence that in sugarbeet (Beta vulgaris L.) erect leaf types had higher net assimilation rate when canopies reached LAI of 2-3. For the same LAI, erect leaf types also had a higher crop growth rate. When both erect and droopy leaf types had LAI of 1, however, no difference in crop growth rate were observed.

In rice Oryza sativa L., Hayashi and Ito (1962) observed that in 14 cultivars, the steeper the inclination of the leaves, the greater the crop growth rate and LAI. Using an erect leaf cultivar, Matsushima et al. (1964) used a mechanical method to cause the leaves to droop. The photosynthetic rate was 34% lower in the droopy leaf treatment. In the second experiment, leaves of a droopy leaf cultivar were mechanically manipulated to be erect. The photosynthetic rate of the erect leaf treatment was 64% higher than the original droopy leaf type. Tanaka et al. (1969) later repeated the experiment conducted by Matsushima et al. (1964) for photosynthesis after flowering. Lower leaves were heavily shaded and crop photosynthetic rate at full sun light and dry matter accumulation were reduced by 38% in the droopy leaf treatment when compared to the normal erect leaf plants.

The effects of leaf angle on yields of barley (Hordeum vulgare L.) have been extensively evaluated. Pearce et al (1967) used barley seedlings grown in seed boxes tilted at various angles to direct leaves and stems at different angles. Large differences in extinction coefficient and photosynthetic rates between treatments were found. At high LAIs, the more erect canopies had higher photosynthetic rates than the more droopy types. Gardener (1966) compared the growth rates of three erect and three droopy leaf barley cultivars. At high LAIs, light was shown to be more uniformly distributed within erect than droopy leaf canopies. Crop growth rates were on average 19% greater than those of droopy leaf cultivars. Early in the season, however, droopy leaf cultivars grew faster than the erect leaf types due to greater light absorption during the early stages. Berhadhl et al. (1972) compared related lines derived from two barley crosses generated from parents having contrasting leaf types. No differences in flag leaf photosynthetic rate per unit leaf area and mean canopy photosynthetic rate were found between the contrasting lines although light penetration was greater in erect leaf group.

In forage grasses, Hunt and Cooper (1967) compared the canopy growth of seven forage grass species with contrasting growth habit, before the first cutting. The long, erect leaf types had the highest photosynthetic rate and crop growth rates. Moreover, Cooper et al. (1970) reported that erect leaf cultivars from six contrasting forage grass species had a larger critical LAI, the maximum LAI attained by the crop, higher maximum crop growth rate, and better light transmission. Maximum crop growth rate was negatively correlated with extinction coefficients, and positively correlated with critical LAI so that the more erect the growth habit the greater the crop growth rate.

Puckride and Ratkowsky (1971) compared photosynthetic rates of two wheat (Triticum aestivum L.) cultivars with contrasting leaf types. No difference in photosynthetic rate was found with LAI of six when cultivars were grown under high solar radiation. However, no quantification of actual differences in canopy architecture were reported for these two contrasting lines. Austin et al (1976) demonstrated that canopy net photosynthesis was consistently higher in erect than in droopy leaf cultivars at high LAI. The differences in photosynthetic rates were due to a greater light penetration into the canopy and longer longevity of lower leaves. Recently, Green (1988) compared five winter wheat cultivars with contrasting leaf inclination for growth analyses. Differences in extinction coefficients were observed among cultivars. The author found that while different cultivars absorbed similar amounts of solar radiation, the efficiency by which absorbed radiation was converted into dry matter was higher before anthesis in the erect leaf cultivars with lower extinction coefficients.

However, during grain filling, the efficiency increased in droopy leaf cultivars with high extinction coefficients, such that mean seasonal value was independent of genotypes and extinction coefficient. Similar results were found for crop growth rate. As a result, variations between erect and droopy leaf types in grain yield were small. The results of this experiment raised the question of whether erect leaf has any impact on grain yield in wheat.

Effects of Leaf Angle on Grain Yield

Whether leaf angle affects grain yield in all cereals remains controversial. The search for such effects has been difficult, as the critical test would require isogenic lines differing only in leaf erectness. However, isogenic lines are available only in a few crops due to the time required to generate such experimental materials.

For rice, there is convincing evidence that erect leaf type can lead to higher grain yield. Tanaka et al. (1969) compared the effect of an erect leaf cultivar with an artificially-drooped treatment where small weights were attached to the leaf tips of the erect leaf cultivar. The erect leaf cultivar had a grain yield 33% higher than that of the artificially drooped rice. The percentage of grains ripened was the most affected by the droopy leaf treatment. The effect of droopiness on the percentage of grain ripening in rice was also reported by Tanaka and Matsushima (1971). Change and Tagumpay (1970) compared random F7 lines resulting from a cross between Peta, a tall indica type rice cultivar with droopy leaves, and I-geo-tze, a japonica type semidwarf with erect leaves and a high yield potential. Progenies were divided into three height groups: shorts, intermediate, and tall. Low grain yield was closely associated with tall, droopy leaf type, while associations between high grain yield and leaf erectness were found for all height groups. Moreover, erect flag leaves had the largest positive direct contribution to grain yield within the semi-dwarf group. Results from this experiment are not surprising since the association between high grain yield and erect leaf is already demonstrated in the erect leaf parent, I-geo-Tze.

As observed by Tanner et al. (1966) among 300 barley, wheat, and oat (Avena sativa L.) lines, the association between leaf erectness and grain yield was very striking. In a different study, Tanner (1969) observed that under good weed control, short stature barley lines with extreme upright leaves yielded as well as check cultivars. Without weed control, the erect leaf genotypes suffered extreme yield loss. Two barley cultivars with similar photosynthetic rates were compared by Angus et al. (1972). The droopy leaf cultivar outyielded the erect leaf type at both high and low seed densities. A positive result was reported by Berhadhl et al. (1972) when related lines derived from the same cross between erect and droopy leaf parents were compared. The erect leaf group outyielded the droopy leaf group, although no differences in photosynthetic rates were observed. The greater number of spikes/area among erect leaf lines were sufficient to offset the larger grain weight and grains/spike in the droopy leaf lines. The authors suggested that enhancing light penetration into the canopy favors development of larger numbers of culms bearing grains. Recently, Tungland et al. (1987) reported results from five cycles of crossing and selection for incorporating erect leaf angle into adapted barleys. No differences in grain yield were found between erect leaf lines and check cultivars--Morex, Robust, Glenn, and Manker. However, when comparisons were made between erect and droopy leaf groups from two populations, a difference was found in one population where droopy leaf outyielded erect leaf lines. No differences between populations were observed. Moreover, yield responses at three planting rates were similar between the contrasting leaf types.

In comparing erect and droopy leaf wheat cultivars, Austin et al (1976) found no consistent differences in grain yield, although photosynthetic rate were higher in erect leaf cultivars. This was due to differences in the quantities of stem reserves of assimilates translocated into spikes. In contrast, Stoskopf (1967) reported yield advantages of erect leaf wheat cultivars when grown in narrow rows. Upright leaf cultivars showed 7-13% higher grain yield than the tall droopy leaf cultivar. The author suggested that upright leaf cultivars tolerate higher plant density, presumably by reducing shading effects on lower leaves. However, by comparing wheat lines derived from the same cross with contrasting leaf erectness, Innes and Blackwell (1983) reported that erect leaf lines outyielded droopy leaf lines at lower plant densities but not at high densities. Erect leaf lines also outyielded droopy leaf lines in fully irrigated as well as drought conditions, which lead the authors to conclude that the superiority of erect leaf lines was the consequence of inherently higher water use efficiency in the erect leaf parent. They also found that erect leaf lines had lower harvest index, longer leaf longevity, and higher grain weight than droopy leaf lines. Recently, Davidson and Sayre (1988) compared two pairs of isogenic lines of durum wheat (Triticum aestivum L.) for leaf erectness. The droopy leaf line outyielded its erect leaf counterpart in one pair but no difference was observed in the other pair. No consistent relationships of in yield components with leaf type were observed.

In maize Zea mays L., a C_4 plant, effects of erect leaf on photosynthetic rate are not expected to be high (Hays and Walker, 1989). This statement is supported by results from Moss and Musgrave (1971) who compared photosynthetic rates of a pair of isogenic lines for leaf erectness conditioned by liguless gene. No differences in photosynthetic rates were observed in the period of two months before flowering period. However, Stintson and Moss (1960) observed a high proportion of barren plants in droopy leaf cultivars. In an experiment where droopy leaves were artificially held at 20 degree from vertical, Pendleton et al. (1968) found that erect leaf treatments did show grain yield advantages. When leaves above the cob were held erect, 14% greater grain yield was observed as compared to 7% increased when all leaves were held erect. Winter and Ohlrogge (1973) conducted a similar experiment at various plant densities. Grain yield reduction was observed at low densities when leaves were held erect. At high densities, the erect leaf stand did outyield the normal leaf treatment. No differences were observed when the two canopy types were compared at their optimum plant densities in three seasons. Hopper and

Anderson (1970) also reported that erect leaf genotypes outyielded the droopy leaf isoline by 38% at 128,000 plants/ha while at 32,000 plants/ha droopy leaf lines outyielded the erect leaf counterparts by 22%. Lambert and Johnson (1978) concluded that, as a C_4 crop, leaf angle in maize would have a less pronounced influence on photosynthesis and grain yield than in C_3 small grains. The effects of leaf angle may interact with plant density through shading, thus affecting the synchrony of tassel and silk emergence. This would influence the success of pollination.

Genetics of Canopy Architectural Traits

A thorough understanding genetic mechanisms underlining traits affecting canopy architecture is required for effective selection.

Fowler and Rasmusson (1969) studied the inheritance of leaf area for flag and the two adjacent lower leaves in barley. The mean leaf area of F1's was usually intermediate to parental means. Narrow-sense heritability estimates, based on F4 on F3 regression, were in the range of 18 to 73%. Barker (1970) reported narrow-sense heritability estimates for leaf angle in F2 and F3 generations of three barley crosses ranging from 20 to 60%.

In wheat, Yadav (1987) investigated the inheritance of flag leaf length using F1 and F2 resulting from a cross between a long and short flag leaf parents. The F1 plants had long flag leaves while the F2 individuals segregated to a close ratio of 9 long and 7 short flag leaves. The author concluded that flag leaf length in this particular wheat cross was controlled by two dominant complementary genes. By comparing five wheat cultivars for traits affecting growth and development, Lupton et al. (1967) reported broad-sense heritability estimates for leaf area and its components in the range of 0 to 70%. Hsu and Walton (1969) studied the inheritance of morphological traits in a five parent diallel cross of spring wheat cultivars. The results indicated that additive genetic variance constituted a large part of the total genetic variance with some degree of dominance for flag leaf length.

Aquino and Jenning (1966) studied the inheritance of leaf habit in rice in F1, reciprocal backcross, F2, and F3 generations resulting from a cross of a tall, leafy and a short, erect leaf parents. The short, stiff, and upright leaf habit was controlled by a single gene. Edwards (1970) investigated genetic mechanisms underlying leaf geometry and growth in F1 and F2 generations resulting from all possible crosses between four lines derived from the same population of Lolium perenne. Non-additive effects controlling total leaf area, individual leaf size and its length and width were reported. The rate of total leaf formation and leaf size showed the highest heterosis. In a 6 x 6 diallel of lines derived from a population of Lolium multiflorum, Edwards and Emara (1970) found broad-sense heritabiliy estimates for leaf area in the range of 40 to 70%, while the values for narrow-sense heritability were in the range of 7 to 40%.

In conclusion, the effects of erect leaf canopy remains unclear. The controversy in the literature may be the result of differences in i) criteria in quantifying erect leaf habit, ii) leaf area index, iii) parental sources including erect and droopy leaf parents, and iv) genetic background other than upright leaf habit.

CHAPTER I

Influence of Leaf Types on Canopy Architecture and Grain Yield in Selected Crosses of Spring Wheat *Triticum aestivum* L.

I. Effects of Parental Sources on the Productivity of F6:2 Progenies.

ABSTRACT

The effect of erect leaf canopy on enhancing grain yield in wheat remains unclear. The objective of this study was to investigate the effects parental germplasm on the performance of progenies. Randomly selected F6:2 lines from crosses between two erect and two droopy leaf spring wheat parents were evaluated for nine traits associated with canopy architecture to determine their influence on the components of yield and grain yield. The experiment was carried out at Centro de Investigacions Agricola del Nororeste (CIANO) located near Obregon, Mexico.

No consistent differences in grain yield were observed between canopy types when all F6:2 lines were considered. However, differences were detected when the parental sources were considered. Some parents had more impact on one leaf type of F6:2 lines than the other. Seri 82 x Asio was the highest yielding cross from which most top yielding entries were derived. Results from phenotypic correlations indicate that positive complementary relationships between harvest index, grains/m^2, and 100 kernel weight contributed to grain yield in this cross. Therefore, the parental source of erect leaves is crucial in developing high yielding lines.

Erect leaf lines were included in the highest and lowest yielding groups indicating that selection may be effective in manipulating leaf canopy into current high yielding droopy leaf cultivars.

INTRODUCTION

Plant breeders and physiologists have attempted to enhance photosynthetic efficiency by manipulating the crop canopy to intercept more light. Hay and Walker (1989) noted that photosynthetic efficiency could be increased if the angle of the leaves were erect so that the irradiance incident upon the leaf surface is reduced below the saturation point at the top of the canopy. Additionally more more photosynthetic active radiation (PAR) could be available to the lower leaves, which would contribute more to the total biomass of the crop.

Evidence supporting the role of erect leaves in enhancing grain yield in cereals have been inconclusive. In rice Oryza sativa L., Yoshida (1972) demonstrated the clear superiority of erectophile canopies. Erect leaf habit was found to directly influence grain yield (Chang and Tagumpay, 1970). Leaf erectness was used as an effective selection criterion for enhancing grain yield in rice (Yoshida, 1972). Austin et al. (1976) demonstrated that net canopy photosynthesis in erectophile wheat (Triticum aestivum L.) cultivars was consistently higher than in lax leaf cultivars. However, there were no consistent differences in ultimate grain yield between the two canopy types. Similar inconclusive results have been reported in barley (Hordeum vulgare L.) (Barker, 1970; Angus et al. 1972) and maize (Zea mays L.) (Pendleton et al., 1968; Ariyanayagam et al. 1974; Russell, 1972; Hicks and Stucker, 1972; Winter and Ohlrogge, 1973)

Research on leaf architecture in wheat has been conducted at the International Maize and Wheat Improvement Center (CIMMYT), in Mexico. Comparisons were made between two pairs of near isogenic durum wheat (Triticum durum L.) lines grown under different plant densities (Davidson and Sayre, 1988). In one pair the broad leaf type had a significantly higher grain yield than its erect leaf counterpart. The authors concluded that there was no biomass or grain yield advantage associated with the erect leaf type. Recently developed bread wheat lines selected by CIMMYT breeders for small, erect leaves have shown some grain yield advantages when grown over many locations. In the 1988 CIMMYT International Spring Wheat Nursery, an erect leaf selection resulting from the cross Hahn*2/Prl was among the top three entries across locations.

Sources of erect leaf habit may influence the outcome of studies when non-isogenic line approaches are utilized. Tungland et al (1987) reported no significant difference for grain yield in barley between erect leaf lines and check cultivars grown under three population densities. Comparisons were made among eight F5 erect leaf lines derived from three populations generated from cyclic crossing between an erect leaf source, CI 6146, and three other lines with horizontal leaf types. Undesirable traits such as culm stiffness, lower leaf number, and late maturing were associated with the erect leaf source, and were responsible for reducing the grain yield potential. Carvalho and Qualset (1978) used a sphaerrococcum wheat cultivar PI 190198, a tall facultative type wheat from Spain, as a source of small, erect leaves. No grain yield advantages were observed for erect leaf lines resulting from crosses with selected droopy leaf parents. The authors concluded that factors other than leaf canopy architecture limited yield improvement. In contrast, Innes and Blackwell (1983) reported small beneficial effects on grain yield of erect leaf over the droopy leaf progenies from the same cross at different plant densities and water regimes. Due to slower leaf senescence, TJB 300/241, the erect leaf parent, contributed high biomass production and leaf area index to the progenies. Therefore, evaluating for effects of upright canopies on grain yield, results may be confounded with the source of erect leaf parents.

In this research, to avoid the bias of comparing different unrelated cultivars and difficulties involved in generating near isogenic lines, randomly selected F6 lines derived from crosses between small, erect and large, droopy leaf parents were compared. Two parents with small, erect leavies were used to determine possible parental effects not related to differences in leaf architecture. By using discriminant function analysis, random progenies were classified into erect and droopy types based on ground cover, canopy leaf angle, light transmission, flag leaf orientation and geometry. Comparisons were then made on leaf senescence, components of yield, harvest index, grain and straw yields.

MATERIALS AND METHODS

Experimental Materials

Experimental populations consisted of F6 lines derived from individual F2 plants resulting from four crosses made between two erect (Parula's' = Prl's' and Asio) and two droopy leaf parents (Seri 82 and Buc's'). Crosses were made in the Centro de Investigaciones Agricolas del Noroeste (CIANO), located in Northwest Mexico, in 1985-1986. F1s were planted in the greenhouse at Oregon State University (OSU) in Corvallis, Oregon. Subsequently, the F2 populations were space-planted on December 10th, 1986, at Yuma, Arizona. One normal spike was picked at random from each F2 plant and planted without threshing in a hill at OSU Crop Science Field Laboratory in 1987. Hills were equally spaced at 50 cm. Six spikes of normal appearance were randomly selected from each hill, and threshed individually. Each F2-derived F4 line (F4:2) was spaced planted in two 3 m rows at CIANO in the winter 1987-88. Three spikes were picked at random from the four most uniform line, threshed and bulked to give individual F5:2 lines, which were multiplied at El Batan, Mexico in the summer 1988. One line was selected from uniform-leaf F5:2 lines derived from the same F2 plant, harvested, threshed, and bulked to obtain the individual F6:2 lines. Lines that were susceptible to diseases, frost damage, or late maturing were discarded. Twenty-eight F6:2 lines from each of the four crosses were chosen at random for evaluation at CIANO, Mexico in the winter 1988-89.

Evaluation of Progenies

Experimental Design The twenty eight F6:2 lines derived from each of four crosses were planted in four replications using a split plot restriction of a randomized complete block design. Crosses were considered main plot treatments and the F6:2 lines from each cross, along with their parents, were considered subplots. Due to the restrictions employed by the irrigation system, each subplot was spatially divided into halves, surrounded by an irrigation canal and border.

A seeding density of 130 kg/ha was used. Each plot consisted of 8 rows, 5 m long with 20 cm between rows. To accommodate combine harvesting, the first and eighth rows were spaced 25 cm from the adjacent rows. Plots were separated by 40 cm. Prior to harvest, plots were trimmed to 4 m length. The six center rows were harvested. The harvested area was 5 m^2.

Growing Conditions Prior to planting, fertilizer in the amount of 150-80-0 kg/ha (N-P-K) was incorporated into the soil. The experiment was planted on 29 November, 1988 at CIANO into dry soil and irrigated on 5 December. The first irrigation date (December 5th, 1988) was used as the reference planting date. An additional 50 kg/ha N (NH_4) was applied as top-dressed 44 days after the first irrigation, followed immediately by a second irrigation. A total of five irrigations were applied during the growing season. Weeds were controlled manually.

Data Collection Ground cover was scored as the percentage of the ground covered by the canopy viewed from a 45 degree angle from vertical and a 45 degree from row direction. Canopy leaf angle was scored visually with greatest emphasis in the uppermost leaves, with reference to an imaginary vertical line. Twice during the season, the photon flux density above and below the crop canopy was measured using a Li-Cor LI-191SB quantum line sensor (μE/sec- /m^2). Measurements were made by holding the sensor over the canopy and then placing the bar at ground level perpendicular to the rows at three places in each plot. The three measurements made inside the canopy were averaged to estimate the plot value. Measurements were made at 60 (stage 8 of Feekes' scale) and 85 (stage 10.5 of Feekes' scale) days after the first irrigation. Ground cover and canopy leaf angle were measured at 50 and 67 days after the first irrigation which corresponded to stage 5 and stage 7 of Feekes' scale, respectively.

Anthesis was defined as the day when half of the plants in the plot exhibited spikes with extruded anthers. Maturity was recorded on a plot basis, when there was a complete loss of chlorophyll from the whole plant part. Flag leaf length (L) was measured from the tip to the collar of the leaf lamina. Width of the flag leaf (W) was measured at the widest point of the leaf. Specific leaf weight (SLW) was the ratio of dry weight to the area of the sampled leaf blades. Length, width and SLW were measured on five flag leaves selected at random from the harvested area of each plot five days after the anthesis date. These leaves were immediately placed in sealed plastic bags, and all samples were stored in a dark, at 4°C.

Apparent leaf orientation value was estimated according to Pepper et al (1977) with some modifications. Flag leaf angle was scored visually as the average angle between the flag leaf lamina and its sheath. Leaf curvature was visually scored as 1/1, 2/3, 1/2, and 1/3: the ratio of the distance from the collar to the curved point compared to whole length of the leaf blade. Apparent leaf orientation value was then calculated from the the flag leaf angle divided by the leaf curvature value. Apparent leaf orientation values were scored at 85 and 105 days after the first irrigation.

Leaf tip burn (LTB) was observed first at the tip of flag leaves and spread around the leaf margin and into the penultimate leaves. Readings were made on a 1-9 scale, with one being no visual symptoms and nine representing severely damaged flag and penultimate leaves. Scorings were made twice, at 90 and 105 days. Leaf senescence of the the third leaf was scored on a 1-10 scale based on ten randomly observed culms. A score of 10 was given when all of the third leaves were senesced. Leaf senescence was scored in the same day at two weeks prior to maturity, when variation was the greatest. Lodging was scored as a percentage of lodged area to the plot area. Lodging was estimated twice, at the grain filling (105 days), when lodging was first apparent, and immediately before harvest.

Grain yield (ADJ_Y) was adjusted to a 12% moisture basis. Moisture content at harvest was determined from a grain sample of approximately 50 gm. Harvest index, biomass, and 100 kernel weight were estimated from the dry aerial portion of 30-35 stems selected at random from the harvested area. The ratio of dried 100 kernel weight to dried biomass of each sample determined harvest index. The plot biomass was derived from plot grain yield divided by harvest index. Straw yield was derived from the difference between biomass and grain yield. Weight of 100 kernels were obtained from a random sample of the combine harvest. Grains/m^2 was calculated from the grain yield/m^2 divided by the 100 kernel weight.

Classification of Progenies

F6:2 lines were classified as to being erect and droopy based on discriminant functions. A multivariate normal distribution among independent variables within each population was assumed. The same variance-covariance matrix of the independent variables was also assumed with each of the two classified groups (Dillion and Goldstein, 1984). Discriminant functions were made specifically for F6:2 lines within each cross by using their parents as model data for contrasting erect and droopy leaf types. The best discriminant functions, where the sum of squared differences between groups were maximized, were constructed from the linear combinations of leaf length, leaf width, percent ground cover at 50 and 67 days, canopy leaf angle at 50 and 67 days, light interception at 60 and 85 days, and apparent orientation value at 105 days. By testing these functions with their parental data, probabilities of misclassification were found between 0 - 6.25%.

RESULTS

Differences between Droopy and Erect Leaf Types

Mean values of F6:2 lines and parents with different leaf types were compared for grain yield, components of yield, and thirtheen other traits (Table I.1). For grain yield, differences were found between the droopy and erect leaf parents. However, these differences were not found in the progenies.

Among the components of grain yield, the droopy leaf parents had lower harvest index, higher grains/m^2, and more kernels/spike than the erect leaf parents. When the F6:2 lines were compared, no differences were found for harvest index, grains/m^2, and 100 kernel weight between leaf type. However, droopy leaf progenies had higher kernels/spike. When comparisons were made between parents and the F6:2 lines, the progeny values were intermediate between the parents except for 100 kernel weight, where both droopy and erect lines exceeded both parents.

The parents differed for several important traits (Table I.1). The erect leaf parents exceeded the droopy leaf parents in leaf tip burning and light transmission. In contrast, the droopy parents had greater values for flag leaf orientation and length, canopy leaf angle and ground cover. When comparisons of traits were made between the parents and F6:2 lines, the progenies tended to be intermediate, except for leaf senescence and days to anthesis, where lower mean values were found. Erect leaf parents were more susceptible to lodging than the droopy leaf parents and progenies. For flag leaf orientation, higher values were found for 85 days.

Among F6:2 lines, all traits related to canopy architecture differed between the erect and droopy leaf types. The erect leaf F6:2 lines were more susceptible to leaf tip burning, flowered earlier, transmitted more light, had shorter and more upright leaves, and had lower ground cover than did the droopy leaf F6:2 lines.

Effects of Parental Background on Grain Yield

The F6:2 erect leaf lines outyielded the droopy leaf types in the lowest yielding cross, Buc/Prl, but were similar in the highest yielding cross, Seri 82 x Asio (Table I.2). When Prl's' was the common parent, the mean grain yields of erect leaf F6:2 lines were higher than the droopy leaf progeny (6772.3 vs 6551.8 kg/ha); when Asio was used as the common erect leaf parent, the opposite was found (6895.5 vs 6999.1 kg/ha). However, F6:2 lines from crosses involving Asio had higher grain yield than those F6:2 lines from Prl's', regardless of leaf types. Thus, the effect of leaf type in the progeny depended partially on the genotype of the erect leaf parents.

Table I.3 shows mean values for eleven traits involving the F6:2 lines derived from Buc's' and Seri 82. Lines with Seri 82 as the common parent had higher grain yield, harvest index and 100 kernel weight, but lower leaf senescence and lodging. The two parents differed for the same traits. Lines with Buc's' as the common droopy leaf parent had more upright leaves and higher light transmission, and flowered earlier, compared to Seri 82 derived lines.

Table I.4 shows values for eleven traits when the two erect leaf parents were used as the common parents. F6:2 lines with Asio as the common parent were higher in grain yield, harvest index, and grains/m^2 compared to lines derived from Prl's'; 100 kernel weight, leaf senescence, and lodging were similar to Prl's' derived lines.

The erect leaf parent Prl's' had higher values for ground cover, leaf angle, and days to anthesis, but not for light transmission and flag leaf orientation. The F6:2 lines derived from Asio, the parent with the lower values, also had lower ground cover, more droopy leaves, and flowered later.

Comparison between Top and Lowest Yielding Lines

The 10 highest yielding entries are presented in Table I.5. Only two droopy leaf genotypes are included. Among the top yielding entries, all but four were derived from the Seri 82xAsio cross. Seven of the 10 lowest yielding entries were erect leaf lines, including parents, Prl's' and Asio (data not shown).

Correlation Analyses

Correlation coefficients among F6:2 lines sharing a common parent were estimated for grain yield, harvest index, grains/m^2, straw yield, leaf senescence, leaf tip burning, and canopy leaf type (erect = 1 and droopy = 2).

For F6:2 lines sharing the droopy leaf parent Buc's'(Table I.6), positive associations were observed between grain yield with grains/m^2, straw yield, and 100 kernel weight. Large negative associations were indicated in 100 kernel weight and grains/m^2, while the largest negative value (-0.79) was found between straw yield and harvest index. Both leaf senescence and leaf tip burning were negatively associated with 100 kernel weight and grain yield. Small, erect leaf type was found associated with leaf tip burning in F6:2 lines with Buc's' as a common droopy parent (-0.48).

In Table I.7, correlation values are provided for F6:2 lines sharing Seri 82. Contrasting results were found between this parental source with that noted for the F6:2 lines with Buc's' as a common parent. The main differences were positive associations between harvest index with grain yield, 100 kernel weight, and grains/m^2, and no associations between leaf tip burning or canopy leaf type with 100 kernel weight and grain yield.

For F6:2 lines with Prl's' as a common parent (Table I.8), positive associations were found between grain yield with 100 kernel weight and straw yield, and the highest positive association was noted for grain yield and grains/m^2 (0.62). A negative association was observed between grains/m^2 and 100 kernel weight while the largest negative correlation was found between harvest index and straw yield (-0.74). Leaf senescence and leaf tip burning had negative associations with grain yield and 100 kernel weight.

For F6:2 lines with Asio as a common parent, similar results can be observed as were indicated for the F6:2 lines with Prl's' as a commom parent. Exceptions were the positive associations between harvest index with grain yield and grains/m^2, and the lack of association between grains/m^2 and 100 kernel weight. Negative associations were also found between leaf senescence with 100 kernel weight and grain yield, whereas only grain yield was negatively associated with leaf tip burning. Small, erect leaf type was also associated with leaf tip burning.

DISCUSSION

The main objective of this study was to describe the effects of leaf erectness on grain yield among randomly derived lines resulting from crosses between erect and droopy leaf parents. No differences in grain yield were found between erect and droopy leaf F6:2 lines, when crosses were not considered. When compared to the erect leaf parents, erect leaf F6:2 lines were higher yielding, had an increased leaf size, leaf angle, ground cover, 100 kernel weight, kernels/spike, and grains/m^2, while maintaining similar high harvest index. In contrast, droopy leaf F6:2 lines showed a reduction in leaf size, had higher light transmission and harvest index, but had lower kernels/spike, grains/m^2, and grain yield when compared to the droopy leaf parents. Leaf size in the erect leaf parents may have been too small to be as productive as their progenies.

Erect leaf F6:2 lines consistently outyielded the droopy leaf lines in crosses where Prl's' was the common erect leaf parent. No differences in grain yield were found between the two leaf types for crosses involving Asio as the common erect leaf parent. However, all F6:2 lines involving Asio had higher grain yield than those lines from crosses involving Prl's'. Moreover, the majority of the top yielding entries were erect leaf F6:2 lines from crosses involving Asio as the common erect leaf parent. Prl's' apparently had more impact on erect than droopy leaf progenies, while Asio may have contributed high productivity to descendent F6:2 lines, regardless of leaf type. The effect of Asio appeared to be high grains/m^2 without a reduction in 100 kernel weight.

Of the two droopy leaf parents, Seri 82 had the greatest yield potential. Positive associations were found between harvest index with both grain yield and grains/m^2 in F6:2 lines from crosses involving Seri 82. This suggests that positive complementary relationships between harvest index, grains/m^2, and 100 kernel weight enhanced the productivity in the SerixAsio cross. Fischer (1975) found that shading during rapid spike growth influenced grains/m^2 by affecting both spikes/m^2 and kernels/spikelet. Perhaps an indirect impact of erect leaf on grain yield could be increased grains/m^2. However, in crosses involving upright leaf Asio, the droopy leaf F6:2 lines had higher grains/m^2 than their erect leaf F6:2 counterparts. Therefore, the contribution from Asio was not related to upright leaves allowing greater grains/m^2. Rather, both droopy leaf parents had higher grains/m^2 than the erect leaf parents, and generally inherited that ability to their progeny. Eslick and Hockett (1974) pointed out that a genetic background which complements the normal trait (droopy leaves) may not complement a contrasting trait (erect leaves). Cooper (1975) suggested that an optimum genetic background must be "designed" for a yield trait to express itself appropriately. In the present study, the genetic background of Seri 82/Kvz was optimum for their progenies to express yielding potential regardless of leaf type.

Leaf Tip Burning

One of the disadvantage observed with the erect leaf genotypes was the association with leaf tip burning. No mention of such an association was found in the literature. In this study i) the erect leaf parents and F6:2 lines showed a higher susceptibility to leaf tip burning, and ii) there was also positive associations between leaf tip burning with high light transmission and erect leaf angle. Negative associations between leaf tip burning with grain yield and its components were found only among erect leaf F6:2 lines. The relationship between the rate of evaporation from leaf surface and leaf tip burning and leaf angle may be related to leaf size. Small leaves are more susceptible to convective energy exchange (Gates, 1964) which may result in more leaf tip burning. Thus, greater water loss from the smaller upright leaves in the erect leaf lines may have been the cause of the greater leaf tip burning in those lines. Leaf tip burning was parent specific. Therefore, parental materials need to be studied prior to their being used in crossing programs.

Breeding Strategies

Rasmusson (1987) suggests that the greatest challenge in ideotype breeding is deciding which traits should be included. Our results indicate that parental sources can be crucial to the success of a breeding program aiming at enhancing grain yield potential through erect leaf canopy. Although no direct effect of leaf erectness on grain yield was found, results did show indirect effects through components of grain yield such as grains/m^2, harvest index, and 100 kernel weight.

Some individual lines in this study did show higher yielding potential than the best parent, Seri 82. The fact that most of the top and lowest yielding lines were also erect leaf type suggesting that selection for high grain yield among erect leaf lines may identify high yielding lines from segregating populations resulting from crosses between productive erect and droopy parents. Trenbath and Angus (1975) suggested that if erect leaf affected yield, selections made on the basis of yield from a wide range of genotypes should tend to have erect leaves. This concept ignores the fact that erect leaf genes must be in a background of high yield potential to begin with and, that they will be expressed favorably in crosses only if complementary genes are found in the other parent. Trenbath and Angus (1975) pointed out that plant density, water supply, light intensity, and nitrogen supply influence the pattern of leaf size and inclination. Therefore, selection for erect leaf may need to be practiced under solid stand conditions, and simultaneously with other yield related traits. In order to avoid the effects of spaced planting conditions, selection may need to be delayed to a generation when there will be sufficient seed for solid stand planting.

Table I.1. Summary of mean values for parents and their progenies from four crosses and parents with contrasting leaf types for grain yield, harvest index, grains/m^2, 100 kernel weight, leaf senescence, leaf tip burning, days to anthesis, light transmission, flag leaf orientation, flag leaf length, canopy leaf angle, ground cover at CIANO, Mexico 1988-89.

Traits	Parents		F6:2 Progenies	
N	Droopy (32)	Erect (32)	Droopy (220)	Erect (228)
Grain yield (kg/ha)	6949.0^{A1}	5471.9^{A3}	6775.4^{A2}	6833.9^{A2}
Harvest index (%)	45.9^{B2}	51.3^{B1}	49.5^{B1}	50.2^{B1}
Grains/m^2	21713.2^{D1}	17556.8^{D3}	20021.0^{D2}	19930.4^{D2}
100 Kernel weight (g)	3.2^{E2}	3.1^{E2}	3.4^{E1}	3.4^{E1}
Kernels/spike	69.3^{F1}	49.1^{F4}	54.8^{F2}	53.5^{F3}
Lodging (at maturity)	36.6^{Q2}	84.0^{Q1}	43.0^{Q2}	30.5^{Q2}
Leaf senescence	3.3^{G1}	3.7^{G1}	2.3^{G2}	2.2^{G2}
Leaf tip burning	2.3^{N3}	4.5^{N1}	3.6^{N2}	4.2^{N1}
Days to anthesis	80.9^{J1}	80.8^{J1}	76.8^{J2}	74.9^{J2}
Light transmission (%, 65 days)	1.3^{K2}	2.1^{K1}	1.7^{K2}	2.4^{K1}
Light transmission (%, 85 days)	1.0^{O4}	1.2^{O3}	1.7^{O2}	2.5^{O1}
Flag leaf orientation (85 days)	45.0^{H3}	27.9^{H4}	74.6^{H1}	59.7^{H2}
Flag leaf orientation (105 days)	98.7^{N1}	74.3^{N2}	96.5^{N1}	74.7^{N2}
Flag leaf length (cm)	290.9^{I1}	224.7^{I3}	235.6^{I2}	225.5^{I3}
Canopy leaf angle (50 days)	47.8^{L1}	29.5^{L3}	49.7^{L1}	42.6^{L2}
Ground cover (%, 50 days)	88.8^{M1}	80.8^{M3}	89.6^{M1}	85.4^{M2}
Canopy leaf angle (67 days)	46.0^{P1}	31.7^{P3}	44.9^{P1}	37.9^{P2}
Ground cover (%, 67 days)	98.5^{NS}	96.6	98.1	96.8

Note: Values superscribed by the same letter but different numeric are different at $P \leq 0.05$ (LSD test).

N = Number of observations for mean.

Table I.2. Summary of mean values from F6:2 lines derived from four crosses with contrasting canopy types for grain yield at CIANO, Mexico 1988-89.

Droopy leaf parent	Canopy type	Erect leaf parent		Progeny mean
		Parula's'	Casio	
Buc's'	Erect	6521.2^{A1}	6550.8^{B2}	6536.0^{F3}
	N	(64)	(60)	(124)
	Droopy	6323.4^{A2}	6870.1^{B1}	6596.8^{F3}
	N	(48)	(52)	(100)
Seri 82	Erect	7023.3^{D1}	7240.2^{E1}	7131.8^{F1}
	N	(48)	(56)	(104)
	Droopy	6780.1^{D2}	7128.0^{E1}	6954.1F2
	N	(64)	(56)	(110)
	Erect mean	6772.3^{G3}	6895.5^{G2}	6833.9^{H1}
	N	(112)	(116)	(228)
	Droopy mean	6551.8^{G4}	6999.1^{G1}	6775.4^{H1}
	N	(112)	(108)	(220)

Note: Values superscribed by the same letter but different numeric are different at $P \leq 0.05$ (LSD test)
N = number of observations for mean.

Table I.3. Mean values for F6:2 lines from crosses involving a common droopy leaf parent for grain yield, harvest index, grains/m^2, 100 kernel weight, leaf senescence, days to anthesis, flag leaf orientation, light transmission, leaf angle, ground cover, and lodging at CIANO, Mexico 1988-89.

	Common parent	N	Grain yield kg/ha	Harvest index %	Grains per m^2	100 Kernel weight g	Leaf senesc	Anthesis days	Flag leaf orientate degree 85 d	Light trans % 85 d	Leaf angle degree 50 d	Ground cover % 50 d	Lodging % at maturity
Parents	Buc's'	16	6288.9^{A3}	41.7^{C3}	21685.9^{D1}	2.9^{E3}	5.7^{F1}	80.7^{G1}	45.0^{H3}	0.82^{I3}	39.4^{J3}	86.3^{K2}	64.1^{L1}
	Seri 82	16	7609.3^{A1}	50.2^{C1}	21740.9^{D1}	3.5^{E1}	0.9^{F3}	81.2^{G1}	45.1^{H3}	1.14^{I3}	56.3^{J1}	91.3^{K1}	9.1^{L4}
F6:2 line	Buc's'	224	6566.4^{A3}	50.2^{C2}	19898.2^{D1}	3.3^{E2}	3.2^{F2}	76.9^{G3}	60.4^{H2}	2.10^{I1}	41.0^{J3}	86.3^{K2}	45.5^{L2}
	Seri 82	224	6843.0^{A2}	51.6^{C1}	19551.4^{D1}	3.5^{E1}	1.5^{F3}	78.7^{G2}	66.5^{H1}	1.90^{I2}	49.6^{J2}	88.4^{K2}	28.6^{L3}

Note: Mean values denoted by the same letter but different numeric are different at $P \leq 0.05$ (LSD test).
N = number of observations.

Table I.4. Mean values for F6:2 lines from crosses involving a common erect leaf parent for grain yield, harvest index, grains/m^2, 100 kernel weight, leaf senescence, days to anthesis, flag leaf orientation, light transmission, leaf angle, ground cover, and lodging at CIANO, Mexico 1988-89.

	Common parent	N	Grain yield kg/ha	Harvest index %	Grains per m^2	100 Kernel weight g	Leaf senesc	Anthesis days	Flag leaf orientate degree 85 d	Light trans % 85 d	Leaf angle degree 50 d	Ground cover % 50 d	Lodging % at maturity
Parents	Prl's'	16	5226.2^{A4}	49.3^{C2}	15837.0^{D3}	3.3^{E2}	2.8^{F2}	81.2^{G1}	22.1^{H3}	0.97^{I2}	36.3^{J3}	90.0^{K1}	79.7^{L1}
	Casio	16	5717.6^{A3}	52.3^{C1}	19058.7^{D2}	3.0^{E3}	4.7^{F1}	80.5^{G2}	33.8^{H3}	1.37^{I2}	22.4^{J4}	70.0^{K3}	88.2^{L1}
F6:2 line	Prl's'	224	6662.1^{A2}	48.5^{C2}	19594.4^{D2}	3.4^{E1}	1.8^{F2}	77.3^{G4}	51.3^{H2}	2.00^{I1}	43.5^{J2}	88.6^{K1}	39.9^{L2}
	Casio	224	6947.3^{A1}	51.6^{C1}	20433.2^{D1}	3.4^{E1}	2.8^{F2}	78.2^{G3}	75.1^{H1}	2.00^{I1}	47.0^{J1}	86.1^{K2}	33.7^{L2}

Note: Mean values superscribed by the same letter but different numeric are different at $P \leq 0.05$ (LSD test).
N = number of observations.

Table I.5. Mean values of ten highest yielding F6:2 lines for grain yield, harvest index, grains/m^2, and kernel weight from CIANO, Mexico in 1988-89.

Rank	Cross	Line	Canopy	Grain yield kg/ha	Grains /m^2 %	Harvest index	Kernel weight gm
1.	SerixCasio	#28	E	8642.3	23839.8	55.7	3.63
2.	SerixPrl	#22	E	8333.3	21756.4	52.8	3.83
3.	BucxCasio	#14	E	8118.6	23404.4	52.4	3.47
4.	BucxPrl	#23	E	8115.0	24416.0	45.6	3.34
5.	SerixCasio	#26	E	7938.0	20571.2	57.5	3.86
6.	SerixCasio	#2	E	7911.4	21311.5	51.5	3.73
7.	SerixCasio	#3	D	7871.2	22717.2	53.7	3.51
8.	SerixCasio	#27	E	7749.5	20354.6	55.0	3.76
9.	SerixCasio	#8	D	7718.5	22284.4	50.9	3.49
10.	BucxPrl	#26	E	7681.1	23087.2	48.9	3.33

Note: E = Erect leaf type, D = Droopy leaf type.

Table I.6. Correlation coefficients among 100 kernel weight, grain yield, grains/m^2, straw yield, leaf senescence, leaf tip burning, and leaf type for F6:2 lines from two crosses, having Buc's' as a common parent grown at CIANO, Mexico 1988-89.

	Grain yield	Harvest index	Grains/ m^2	Straw yield	Leaf senescence	Leaf tip burning	Leaf type
100 Kernel weight	0.40**	-0.01	-0.45**	0.26*	-0.46**	-0.33**	-0.05
Grain yield		0.18	0.63**	0.43**	-0.38**	-0.49**	0.05
Harvest index			0.20	-0.79**	0.06	0.13	-0.11
Grains/m^2				0.17	0.02	-0.22	0.10
Straw yield					0.23	-0.39**	0.13
Leaf senescence						0.10	0.24
Leaf tip burning							-0.48**

Note: N=56

*,** denoted significantly different at $P \leq 0.05$ and 0.01, respectively.

Table I.7. Correlation coefficients among 100 kernel weight, grain yield, grains/m^2, straw yield, leaf senesence, leaf tip burning, and leaf type for F6:2 lines from two crosses, having Seri 82 as a common parent grown at CIANO, Mexico 1988-89.

	Grain yield	Harvest index	Grains/ m^2	Straw yield	Leaf senescence	Leaf tip burning	Leaf type
100 Kernel weight	0.33**	0.27*	-0.30*	-0.02	-0.28*	-0.10	-0.20
Grain yield		0.51**	0.79**	0.30*	-0.16	-0.14	-0.20
Harvest index			0.32*	-0.66**	-0.06	-0.10	-0.23
Grains/m^2				0.35**	0.03	-0.07	-0.05
Straw yield					0.03	-0.03	0.12
Leaf senescence						0.25*	0.03
Leaf tip burning							-0.23

Note: N=56

*,** denoted significantly different at $P \leq 0.05$ and 0.01, respectively.

Table I.8. Correlation coefficients 100 among kernel weight, grain yield, grains/m^2, straw yield, leaf senesence, leaf tip burning, and leaf type for F6:2 lines from two crosses, having Parula's' as a common parent grown at CIANO, Mexico 1988-89.

	Grain yield	Harvest index	Grains/ m^2	Straw yield	Leaf senescence	Leaf tip burning	Leaf type
100 Kernel weight	0.41**	0.21	-0.45**	0.10	-0.56**	-0.44**	0.06
Grain yield		0.22	0.62**	0.49**	-0.51**	-0.42**	0.04
Harvest index			0.04	-0.74**	-0.31*	-0.02	-0.09
Grains/m^2				0.38**	0.00	-0.07	0.00
Straw yield					-0.01	-0.27*	0.11
Leaf senescence						0.28*	-0.01
Leaf tip burning							-0.28*

Note: N=56

*,** denoted significantly different at $P \leq 0.05$ and 0.01, respectively.

Table I.9. Correlation coefficients among 100 kernel weight, grain yield, grains/m^2, straw yield, leaf senesence, leaf tip burning, and leaf type for F6:2 lines from two crosses, having Casio as a common parent grown at CIANO, Mexico 1988-89.

	Grain yield	Harvest index	Grains/ m^2	Straw yield	Leaf senescence	Leaf tip burning	Leaf type
100 Kernel weight	0.54**	0.23	-0.12	0.22	-0.40**	-0.03	-0.10
Grain yield		0.52**	0.77**	0.32*	-0.37**	-0.27*	0.08
Harvest index			0.42**	-0.63**	-0.12	-0.05	0.08
Grains/m^2				0.23	-0.13	-0.28*	0.17
Straw yield					-0.15	-0.16	-0.02
Leaf senescence						-0.06	0.15
Leaf tip burning							-0.40**

Note: N=56

*,** denoted significantly different at $P \leq 0.05$ and 0.01, respectively.

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CHAPTER II

Influence of Leaf Types on Canopy Architecture and Grain Yield in Selected Crosses of Spring Wheat *Triticum aestivum* L.

II. Comparison between Paired F6:2 lines for Contrasting Leaf Types.

ABSTRACT

The effect of leaf angle on grain yield in wheat is controversial. Information was obtained by comparing contrasting paired F6 lines derived from individual F2 plants differing in leaf architecture. The objective was to provide a similar genetic background for precise comparisons. The experiment was conducted at Centro de Investigaciones Agricolas del Noroeste (CIANO), Sonora, Mexico. Comparisons were made on percent ground cover, efficiency of converting solar radiation into dry matter, crop growth rate, extinction coefficient, leaf area index (LAI), leaf angle and size, leaf senescence, components of yield, and grain yield.

Erect leaf architecture in these experimental populations had beneficial effects on grain yield. Such effects, however, were not due to the difference in efficiency of converting solar radiation into dry matter or crop growth rate but rather to higher grains/m^2, harvest index, and slower leaf senescence in erect leaf lines. The erect leaf group had more grains/m^2, but smaller grain size. In spite of a smaller leaf size, erect leaf types maintained as high LAI as the more droopy leaf types and shown benefit on crop growth rate during 55-95 days. Erect leaf offers a yield advantage in a genetic background and environment that allows for accumulation of high LAI. The paired derived-line approach may be useful as an alternative method for compairing effects of physiological traits affecting canopy architecture and grain yield potential.

INTRODUCTION

Leaf inclination was first suggested as an important factor for enhancing dry matter production and grain yield by Boysen-Jensen (1932, 1949). His hypothesis was that a dense crop with erect leaves would have a higher photosynthetic rate per unit ground area than one with horizontal leaves. The search for the effects of leaf inclination on the processes leading to grain yield has proven to be difficult because critical tests require genetic lines which are nearly identical in all aspects except leaf inclination.

Experimental results with crop cultivars which differ in leaf inclination have been inconclusive. Watson and Witts (1959) found in sugarbeet (Beta vulgaris L.) that an erect leaf cultivar had a significantly higher net assimilation rate (NAR) and crop growth rate (CGR) than a droopy leaf type. In forage grasses, Hunt and Cooper (1967) also found that genotypes with long, erect leaves had the highest photosynthetic systems, crop growth rate and a larger critical LAI than the prostrate cultivars. Cooper et al (1970) found that maximum crop growth rate was negatively correlated with extinction coefficient, positively correlated with critical LAI and with the leaf erectness in six forage grasses with contrasting canopy architecture. The more erect the growth habit, the greater the crop growth rate. Moreover, a significant correlation between maximum rates of dry matter production and the LAI required to achieve 95% light interception was also reported in forage grasses (Brougham, 1960). In rice (Oryza sativa L.), Hayashi and Ito (1962) reported that within a group of 14 rice cultivars, the steeper the inclination of the leaves, the greater the crop growth rate and maximum LAI reached. Narrow, upright leaf barleys (Hordeum vulgare L.), although slowly achieving 95% light interception, eventually had a greater LAI and a higher rate of dry matter accumulation than droopy leaf types (Gardener et al., 1964).

In contrast to the positive effects of erect leaf types, Puckridge and Ratkowsky (1971) observed no differences in photosynthetic rate when comparing two wheat cultivars (Triticum aestivum L.) differing in canopy types in a field assimilation chamber, with a LAI of about six and under high solar radiation conditions. Moss and Musgrave (1971), comparing photosynthetic rates between isogenic maize lines (Zea mays L.) differing in leaf angle, found no differences in photosynthetic rate measured for over two months. Sinclair et al. (1971) found no significant differences in the productivity of the maize isogenic lines at LAI of 3.5.

Recently, Green (1989) compared five winter wheat cultivars with contrasting leaf inclination. The author found that, while different cultivars absorbed similar amounts of solar radiation, the efficiency by which absorbed radiation was converted into dry matter was higher before anthesis in cultivars with lower extinction coefficients. However, during the grain filling period, the efficiency increased in cultivars with high extinction coefficients, such that mean seasonal efficiency was independent of genotypes and extinction coefficient. Consequently, variation between erect and droopy leaf types in grain yield was small. Austin et al. (1976) also reported that there were no consistent differences in ultimate grain yield between the two canopy types in wheat due to differences in the quantities of stem reserved assimilates translocated to the spike. In durum wheat (Triticum durum L.), Davidson and Sayre (1988), comparing two near isogenic lines differing in leaf erectness, found that a lax leaf genotype outyielded its erect leaf counterpart. They concluded, however, that differences in components of yield rather than in leaf erectness were responsible for increased grain yield.

According to Loomis and Gerakis (1975) most of these studies failed to see the beneficial effects of erect leaf types by using plant stands with LAI too low to observe any significant differences. As reported by Winter and Ohlrogg (1973) the beneficial effects of these erect leaf maize isogenic lines could only be seen when LAI was more than 3-4. In sugarbeet, Watson and Witts (1959) also found that when LAIs were above 2-3, the erect leaf cultivar had a much higher net assimilation rate (NAR) than that of the lax leaf cultivar. According to mathematical models, Monteith (1965) and de Wit (1965) suggested that with LAIs greater than 3-4, crops with erect leaves will have higher canopy photosynthetic rates than those with lax leaf forms.

This study was undertaken to compare the effect of leaf angle between contrasting F6 wheat lines derived from individual F2 plants of crosses between erect and droopy leaf plants. Comparison of performance are made in closely related lines, differing primarily in leaf angle.

MATERIALS AND METHODS

Experimental Materials

Experimental populations consisted of F6 lines of wheat (Triticum aestivum L.) derived from individual F2 plants resulting from six crosses between erect and droopy leaf parents. The droopy leaf parents were Glennson 81, Seri 82, Buc's', Baya's'/Buc's'; the erect leaf parents were Parula's' (Prl's') and Asio. These parental materials are day-length insensitive spring wheats that require no vernalization. Crosses were made at the Centro de Investigaciones Agricolas del Noroeste (CIANO), located in northwest Mexico, in 1985-1986. F1s were planted in the greenhouse at Oregon State University in Corvallis, Oregon. F2 populations were planted Yuma, Arizona. One normal spike selected at random from each F2 plant was planted in a hill without threshing at Corvallis summer, 1987. Spikes were equally spaced at 50 cm. Six normal appearing spikes were randomly selected from each hill and threshed individually. Late maturing and diseased spikes were discarded. Each F2-derived F4 (F4:2) line was spaced planted in two 3 m rows at CIANO. Three spikes where picked from the four most uniform lines, threshed and bulked to represent the F5:2 line, which were multiplied in CIMMYT, El Batan, Mexico during summer, 1988. From these four F5:2, two lines were chosen based on the differences in leaf angle and/or leaf size. Lines with susceptibility to diseases, frost damage, and late maturing were discarded. The selected lines were harvested and threshed in bulk to obtain the F6:2 lines.

Evaluation of Progenies

Design of Experiment Twenty eight pairs of F6:2 lines representing six crosses were selected on the basis of contrasting leaf size and/or angles. The experimental lines were planted in four replications using a split plot restriction of a randomized complete block design. Twenty eight pairs were considered main plots and the two contrasting progeny type were considered subplots. Subplots were nested within the paired F6:2 lines. Because of the restriction on the irrigation system at the experimental site, plots were planted in halves, accommodated 16 plots, surrounded by irrigation canal and borders.

A seeding density of 130 kg/ha was used. Each plot consisted of eight 5 m rows with 20 cm between rows. To accommodate combine harvesting, the first and eight rows were spaced 25 cm from the adjacent rows. Individual plots were separated by 40 cm. Prior to harvest, plots were trimmed to 3 m and the six central rows were machine-harvested. The harvested area was 3.75 m^2.

Growing Conditions Fertilizer in the amount of 150-80-0 kg/ha (N-P-K) was incorporated into the soil preplant. The material was seeded 29 November in dry soil at a depth of 2.5 cm and irrigated 5 December. The date of the first irrigation is used as the reference planting date. An additional 50 kg/ha N was applied as top-dressed at 44 days. Soil moisture content was monitored and subsequently five additional irrigations were applied. Weeds were controlled manually. Propiconazole (Tilt) was used one time during the grain filling period at a rate of 0.35 l/ha, to control leaf rust (Puccinia recondita).

Data Collection Ground cover was scored as the percentage of the ground covered by the canopy viewed from a 45 degree angle from vertical and 45 degree from row direction. Canopy leaf angle was scored visually, with greatest emphasis on the uppermost leaves, with reference to an imaginary vertical line. Three times during the season, the photon flux density above and below the crop canopy was measured using a Li-Cor LI-191SB quantum line sensor ($\mu E/sec/m^2$). Measurements were made by holding the sensor over the canopy and then placing the bar at ground level perpendicular to the rows at three places in each plot. The three measurements made inside the canopy were averaged to estimate the plot value. Measurements were made at 55, 70, and 95 days. Ground cover and canopy leaf angle were measured at 50 and 67 days which corresponded to tillering and elongation stages, respectively. Because pollen shedding dates varied by 15 days, measurements could not be made at the same stage for every genotype. Therefore, growth stages, apart from anthesis date and maturity, are approximate.

Anthesis was defined as the day when half of the plants in the plot exhibited spikes with extruded anthers. Maturity was recorded when there was a complete loss of chlorophyll from all plant parts. Flag leaf length (L) was measured from the tip to the collar of the leaf lamina. Width of the flag leaf (W) was measured at the widest point of the leaf. Specific leaf weight (SLW) was the ratio of dry weight to the area of the sampled leaf blades. Length, width and SLW were measured on five flag leaves selected at random from the harvested area of each plot five days after the anthesis date. These leaves were immediately placed in sealed plastic bags and all samples were stored in a dark, at 4°C.

Apparent leaf orientation value was estimated according to Pepper et al (1977) with some modifications. Flag leaf angle was scored visually as the average angle between the flag leaf lamina and its sheath. Leaf curvature was visually scored as 1/1, 2/3, 1/2, and 1/3: the ratio of the distance from the collar to the curved point compared to the whole length of the leaf blade. Apparent leaf orientation value was then calculated from the flag leaf angle divided by the leaf curvature value. Apparent leaf orientation values were scored at 85 and 105 days after the first irrigation.

Leaf tip burn (LTB) was first observed at the tip of flag leaves after anthesis and spread around the leaf margin and penultimate leaves. LTB was visually estimated on a 1-9 scale, with one being no symptom and nine representing severely damaged flag and penultimate leaves. Readings were done twice, at 90 and 105 days. Leaf senescence of the third leaf was scored on a 1-10 scale based on ten randomly observed culms. A score of 10 was given when all of the third leaves were senesced. Leaf senescence was scored at two weeks prior to maturity, when variation was the greatest. Lodging was scored as a percentage of lodged area to the plot area. Lodging was scored twice, at the grain filling (105 days), when lodging was first apparent, and immediately before harvest.

Grain yield (ADJ_Y) was adjusted to a 12% moisture content. Moisture content at harvest was determined from a grain sample of approximately 50 gm. Harvest index, biomass, and 100 kernel weight were estimated from dry aerial portion of 30-35 stems selected at random from the harvested area. The ratio of dried 100 kernel weight to biomass of each sample determined harvest index. The plot biomass was derived from plot grain yield divided by harvest index. Straw yield was derived from the difference between biomass and grain yield. Weight of 100 kernels were obtained from a random sample of the combined harvest. Grains/m^2 was calculated from the grain yield/m^2 divided by the 100 kernel weight.

Above ground dry matter was measured on a sample area of 0.30 m^2 sampled from the north end of the plot at 55, 70, 95 days. Samples were taken, within six inner rows, at least 30 cm from the previous sample and 75 cm from the plot end, placed in plastic bags, and stored in dark chamber at 4°C. The final machine harvest avoided these sampling areas. Green area of leaves, stems, and spikes were determined on twenty percent of the shoots from the harvested sample using a Li-COR (LI-300) leaf area meter. Yellow leaves were discarded. The area was calculated from the summation of projected area of one-sided leaves, stems, and spikes. Apparent extinction coefficient (K, Monsi and Saiki, 1953) was calculated as:

$$I/I_o = e^{-KL}$$

$$\log(I/Io) = -KL$$

$$K = -(\log I/I_o)/L$$

Where I/I_o: the ratio of light at the ground level in the canopy (I) to that of the above canopy (Io),

L: Leaf area index,

K: Apparent extinction coefficient.

Extinction coefficient reflects the average leaf inclination of the canopy where canopy with lower extinction coefficient has leaves more erect than canopy with higher extinction coefficient. The average extinction coefficients for each plot were estimated from the regression coefficients of the $\log(I/I_0)$ for the three sampling dates (55, 70, and 95 days) with the respective values for LAIs. The regression lines were constrained to pass through the origin.

The proportion of radiation absorbed, f, was estimated as suggested by Green (1989) as follows:

$$f = (1-(I/I_0))/(1+\rho)$$

ρ : an approximation of the albedo expressed as a constant fraction of "f" with the suggested value of 0.26.

The solar irradiation absorbed was taken from the product of the proportion of radiation absorbed, estimated cumulative total solar irradiation (three year average, Fischer, 1975), and the fraction of total solar radiation which is photosynthetic active radiation (0.5). The estimated cumulative solar radiation up to 55, 70, and 95 days was estimated as 16,900, 22,375, and 28,340 langley/m^2, which would not affect the outcome of the result since the radiation data is a constant fraction for each interval. PAR (Photosynthetic Active Radiation), ϵ_m

(the conversion efficiency of absorbed radiation into biomass), and crop growth rate for 55 - 70 days were estimated as follows:

$PAR_{abs\ 55-70}$ = Total solar radiation $_{55-70}$ x 0.5 x $f_{55,70}$

f 55,70 = Radiation absorbed at 70 - Radiation absorbed at 55

$\epsilon_{(55\text{-}70\ d)}$ = $(TDW_{70} - TDW_{55})/PAR_{abs\ 55-70}$

TDW = Total dry weight

CGR = $(TDW_{70} - TDW_{55})/(70\text{-}55\ \text{days})$

The same methods of estimation were used for 70-95 days. These parameters were estimated based on three measurements made 55, 70, and 95 days after the first irrigation. The average values for each parameter were calculated from the mean values of 55-70 and 70-95 days.

RESULTS

Analyses of Variance

The analysis of variance for selected traits is presented in Table II.1. Differences between replications were found in all traits except for leaf senescence, grain yield, and 100 kernel weight. Large variations due to replications were found for extinction coefficient, efficiency of converting solar radiation into dry matter, and crop growth rate. Differences among pairs and differences between contrasting leaf types within each pair were found for all traits. Overall differences between contrasting leaf types were found for most traits except for extinction coefficient and efficiency of converting solar radiation into dry mattter. The largest variation was found in light interception at 55 days. Similar results for the interaction between pairs and contrasting leaf types can be observed as were found for the contrast within pairs. Significant contrasting leaf types by pair interactions indicated that differences between droopy and erect leaf lines were inconsistent.

Differences between Droopy and Erect Leaf Types

Comparisons between erect and droopy leaf lines for all traits and dates of measurement are given in Table II.2. During canopy formation droopy leaf F6:2 lines covered the ground faster, accumulated more LAI and dry matter, intercepted more solar radiation, and had higher extinction coefficients. During 55-70 days, no differences were found in LAI, light interception, extinction coefficient, and efficiency of converting solar radiation into dry matter, even though droopy leaf lines had a greater estimated ground cover. Erect leaf F6:2 lines accumulated more dry matter than the droopy leaf counterpart and had higher crop growth rate. Flag leaves of droopy lines were larger, but flag leaves of erect leaf F6:2 lines had higher specific leaf weights.

Following anthesis (95 days), droopy leaf lines maintained higher leaf area than their erect leaf counterparts but had lower crop growth rate. During canopy senescence, erect leaf lines had slower leaf senescence, whereas droopy leaf lines were taller and had higher lodging.

Mean Efficiency of Converting Solar Radiation and Crop Growth Rate

Droopy leaf F6:2 lines consistently intercepted more solar radiation before canopy closure, but after canopy closure there was no difference between droopy and erect leaf lines. Erect leaf F6:2 lines accumulated more dry matter and thus had consistently higher crop growth rate, but no differences in mean efficiency of converting solar radiation into dry matter were detected. After canopy formation, but before the canopy closure, the droopy leaf had higher dry matter accumulation and crop growth rate. Therefore, there was an advantage of erect leaf over droopy leaf in terms of crop growth rate.

Grain Yield and Its Components

Differences in grain and straw yield, harvest index, grains/m^2, and 100 kernel weight are presented in Table II.3. Erect leaf F6:2 lines had higher harvest index and grains/m^2, was slower in leaf senescence, had lower 100 kernel weight and straw yield, and greater yield.

Correlation coefficients between grain yield, yield components, and growth parameters are given in Table II.4. The coefficients were calculated from the differences between the mean values of droopy and erect leaf counterparts within each pair. Positive associations were found between grain yield and 100 kernel weight, harvest index, and grains/m^2. Negative associations were found between 100 kernel weight and grains/m^2, and between straw yield and harvest index. Differences in efficiency of converting solar radiation into dry matter and crop growth rate did not show any associations with grain yield and yield components, except a positive correlation between crop growth rate and grain weight. Differences in ground cover at 67 days showed a negative association with grain yield, but no associations were detected between ground cover with any yield components.

DISCUSSION

Erect leaves showed a slight beneficial effect on grain yield in this study. The effect, however, was independent of efficiency of converting solar radiation into dry matter or crop growth rate, and was due to the variation in grains/m^2, harvest index, and third leaf senescence. The independence of efficiency of converting solar radiation into dry matter, crop growth rate, and grain yield was also reported by Green (1989). In his experiment, the efficiency of converting solar radiation into dry matter and crop growth rate were higher before anthesis in cultivars with more erect leaf habit, but lower after anthesis in the same cultivar; thus, the season means were independent of cultivars. In this experiment, although no differences in efficiency of converting solar radiation into dry matter were observed during 55-95 days, erect leaf did show higher crop growth rate than the droopy leaf counterpart.

Small differences in extinction coefficients observed between paired progenies may be caused by i) the modest variation in leaf erectness within F2-derived lines, ii) the inability to visually recognize differences in leaf inclination at the whole plant level during segregating generations, iii) differences in leaf sizes, and iv) leaf angle may be different only on the upper canopy layer but similar on the lower layer. As pointed out by Ledent and Moss (1977), leaf angle may increase downward through the depth of canopy, so that light is efficiently intercepted by both canopy types. Austin et al. (1976) also reported their erect leaf material was different from the lax leaf materials only on the flag and penultimate leaves. This may have been the case with the lines used in this study, since no differences in light transmissions were detected after the canopies were at full light interception. It can be speculated that light transmission measured at the ground level may not be sensitive enough to reflect small differences in leaf angle on the lower layer of the canopy. Therefore, visual classification into erect-droopy leaf types may not be closely associated with differences in extinction coefficients. In order to see greater differences in extinction coefficients, a more laborious method originally used by Monsi and Saeki (1953) is more appropriate if small differences in extinction coefficient need to be demonstrated.

That differences in ground cover at 67 days showed a significant negative association with grain yield was surprising, because the relationship at 50 days was not significant. Rapid ground cover, which can be observed in droopy leaf types, may create overshading conditions unfavorable for some physiological processes leading to high grain yield. Tanner (1969) found that, under good weed control, a short stature genotype with extreme upright leaf lines yielded equal to the check varieties, while under no weed control, the same genotype was greatly reduced in grain yield. Since weeds were controlled in this study, the beneficial effects of more upright leaf type on grain yield could not be limited by competition from weeds. Therefore, the negative association between grain yield and ground cover may be the reflection of the association of more upright leaf type with grain yield. However, the differences between droopy and erect leaf counterparts were small, being only 4% before and 1.5% after canopy closure. From the field observation, most of erect leaf genotypes accomplished a two layer canopy characteristic early in the season, by forming more droopy leaves at the lower layer of the canopy. Eventually, such canopy development might approach an 'ideal' canopy as described by Verhagen et al (1963) and Duncan (1971).

Austin et al (1976) found that erect leaf genotypes had a longer leaf area duration, and thus maintained a high leaf area index throughout the season. In this study, leaf senescence was slower in the erect leaf lines. However, Green (1989) found no differences in leaf duration among winter wheat cultivars differing in extinction coefficients. As shown by Rawson and Hofstra (1968), a significant amount of photosynthate was mobilized from lower leaves into roots and tiller ears during grain filling period. Therefore, longer leaf duration is an important pleiotropic effect of erect leaf habit in maintaining high leaf area index after anthesis, which in turn has beneficial effects on grain yield.

In the present study, the beneficial effect of erect leaf type was clearly shown by enhancing grains/m2. In a shading experiment, Fischer (1975) suggested that light conditions during rapid spike growth affects grains/m^2 through spikes/m^2 and grains/spikelet. Berhadl et al (1972) also found that erect leaf affects the ratio of tiller bearing grains. Recently, Fischer (1985) pointed out that, within the same cultivar, small differences in dry matter accumulation in the critical spike growth period (30 days before anthesis) was related to the differences in grains/m^2. In the present study, although erect leaf had 6.7%

more grains/m^2 and 3.2% higher average crop growth rate during 55-95 days, no correlation for the differences within pairs between crop growth rate and grains/m^2 was detected. One hundred kernel weight, instead, did show a large positive association with the differences in mean crop growth rate during 55-95 days. This contradictory results can be explained by large significant contrast by pair interactions detected in all parameters. Therefore, results from comparing within a cultivar can be quite different from results when different genetic backgrounds are involved.

The effects of leaf erectness on grain yield have been difficult to assess, due to the requirement of genetic lines differing only in leaf erectness. Although the near-isogenic line approach permits comparisons of the worth of a contrasting traits without having confounding effects from different genetic background, laborious backcrossing procedure limits the number of pairs to be generated. Eslick and Hockett (1974) pointed out the expressivity of the contrasting traits may be completely masked by an unsuitable genetic background. In the present study, the 28 paired F6:2 lines represent six genetic backgrounds generated from six crosses of erect and droopy leaf parents. The ease of generating genetic materials through random advance of paired lines avoids the effect of limited genetic background in comparisons.

Table II.1. Pertinent F-ratios ($P \leq 0.05$), error mean squares, and coefficients of variation (C.V.) from analyses of variance for light interception at 55 days, mean extinction coefficient (K), mean efficiency of converitng solar radiation into dry matter (ESD), mean crop growth rate (CGR), leaf senescence, grain and straw yiels, harvest index (HI), grains/m^2, and kernel weight at CIANO, Mexico 1988-89.

Source of variation	df	Light intercept %	K	ESD g/ly/m^2	CGR g/m^2/d	Leaf senesc	Grain yield kg/ha	Straw yield kg/ha	HI %	Grains /m^2	Kernel weight g
Replication	3	10.92[1]	27.77	23.67	21.76	ns[2]	ns	4.00	4.3	4.42	ns
Pairs	28	10.32	3.7	5.07	3.67	5.08	7.29	4.97	3.93	3.11	6.94
Error(a)	84	2.64	ns	1.52	1.46	2.01	2.62	1.84	ns	ns	ns
Contrast/Pair	29	12.86	2.51	5.31	4.64	3.6	4.25	1.90	2.64	2.67	3.86
Contrast	1	109.57	ns	ns	4.17	4.37	5.42	2.87	11.22	14.14	7.69
ContrastxPair	28	9.41	2.52	5.49	4.66	3.58	4.21	1.87	2.33	2.26	3.72
Error(b)	87	20.89[3]	0.0034	0.0006	14.922	2.764	213548.34	684234.34	11.76	6960355.4	0.097
C.V.		3.86	11.68	13.1	12.15	37.46	7.63	15.3	6.56	10.22	8.23

1/ F-ratio

2/ non-significant differences at $P \leq 0.05$

3/ Error mean square

Table II.2. Means of paired F6:2 lines with contrasting leaf types for ground cover, leaf inclination, leaf area index (LAI), dry matter accumulation, light interception and absorption, extinction coefficients, growth parameters, days to anthesis, flag leaf orientation and geometry, plant height, lodging, and leaf senescence at CIANO, Mexico 1988-89.

	Days		Unit	Droopy	Erect	SE
Canopy Formation	50	Ground cover	%	86^{A1}	83^{A2}	±0.30
	50	Leaf inclination	degree	42^{B1}	35^{B2}	±0.36
	55	LAI	-	4.60^{C1}	4.33^{C2}	±0.10
	55	Dry matter accumulation	g/m^2	359^{D1}	352^{D2}	±5.2
	55	Light interception	%	85.6^{E1}	83.3^{E2}	±0.43
	55	Extinction coefficient	-	0.47^{F1}	0.45^{F2}	±0.01
Canopy Closure	67	Ground cover	%	98^{H1}	96^{H2}	±0.48
	67	Leaf inclination	degree	42^{I1}	31^{I2}	±0.11
	70	LAI	-	8.98^{NS}	8.99	±0.15
	70	Dry matter accumulation	g/m^2	667^{J2}	679^{J1}	±3.2
	70	Light interception	%	97.7^{NS}	97.2	±0.09
	70	Extinction coefficient	-	0.48^{NS}	0.47	±0.01
	55-70	Efficiency of convert solar:dm	g/ly/m^2	0.109^{NS}	0.107	±0.0017
	55-70	Crop growth rate	g/m^2/d	20.9^{U2}	21.8^{U1}	±0.28
Anthesis		Days to anthesis	day	83^{NS}	83	±0.28
	85	Flag leaf orientation	degree	79^{K1}	55^{K2}	±1.23
		-Flag leaf angle	degree	53.9^{Q1}	50.3^{Q2}	±0.55
		-Flag leaf curvature	-	0.88^{R2}	0.97^{R1}	±0.02
		Flag leaf length	cm	25^{L1}	23^{L2}	±0.17
		Flag leaf width	cm	1.8^{M1}	1.7^{M2}	±0.09
		Specific leaf weight	gm/cm^2	0.51^{N2}	0.54^{N1}	±0.004
Post Anthesis	95	LAI	-	7.58^{O1}	7.32^{O2}	±0.11
	95	Light interception	%	98.55^{NS}	98.13	±0.06
	95	Extinction coefficient	-	0.59^{NS}	0.57	±0.01
	95	Dry matter accumulation	g/m^2	1305^{NS}	1320	±40.0
	70-95	Efficiency convert solar:dm	g/ly/m^2	0.264^{NS}	0.266	±0.005
	70-95	Crop growth rate	g/m^2/d	41.7^{V2}	42.7^{V1}	±0.70
Growth Parameters		Mean extinction coefficient	-	0.50^{NS}	0.50	±0.006
		Mean efficiency convert solar:dm	g/ly/m^2	0.185^{P2}	0.188^{P1}	±0.02
		Mean crop growth rate	g/m^2/d	31.3^{W2}	32.3^{W1}	±0.37
Canopy Senescing	105	Flag leaf orientation	degree	114^{Q1}	73^{Q2}	±5.31
		-Flag leaf angle	degree	77.6^{NS}	67.8	±5.18
		-Flag leaf curvature	-	0.53^{S2}	0.83^{S1}	±0.02
	108	Leaf senescence		4.63^{R1}	4.03^{R2}	±0.16
	114	Plant height	cm	101.07^{S1}	97.37^{S2}	±0.29
	108	Lodging	%	45^{T1}	33^{T2}	±2.26

N=112

Values superscribed by the same letter but different numeric are different at $P \leq 0.05$.

Table II.3. Means of paired F6:2 lines with contrasting leaf types for grain and straw yields, harvest index, grains/m^2, and kernel weight at CIANO, Mexico 1988-90.

Traits	Unit	Droopy	Erect	SE
Grain yield	kg/ha	5751.60^{A2}	6009.07^{A1}	± 43.67
Straw yield	kg/ha	7261.10^{B1}	7025.79^{B2}	± 78.16
Harvest index	%	44.20^{C2}	46.10^{C1}	± 0.33
Grains/m^2	-	17429^{D2}	18604^{D1}	± 249.3
Kernel weight	g	3.30^{E1}	3.23^{E2}	± 0.03

Note: values superscribed by the same letter but different numeric are different at $P \leq 0.05$.

Table II.4. Correlation coefficients at $P \leq 0.05$ for 100 kernel weight, straw yield, harvest index, grain/m^2, leaf senescence, mean efficiency of converting solar radiation into dry matter (ESD), mean crop growth rate (CGR), and ground cover at 67 days from CIANO, Mexico 1988-89.

	Kernel weight	STRAW yield	Harvest index	Grains /m^2	Leaf senesc	ESD	CGR	Ground cover
Grain yield	0.57**	0.26	0.51**	0.41*	-0.29	-0.03	0.24	-0.47**
Kernel weight		0.30	0.16	-0.51**	-0.07	0.29	0.49**	-0.22
Straw yield			-0.69**	-0.03	-0.01	0.09	0.22	-0.12
Harvest index				0.33	-0.23	-0.10	0.01	-0.28
Grains/m^2					-0.20	-0.34	-0.27	-0.29
Leaf senescence						0.29	0.18	0.11
ESD							0.75	0.10
CGR								-0.02

Note: N=27

*,** denoted significantly different at $P \leq 0.05$ and 0.01, respectively.

ESD: mean efficiency of converting solar radiation into dry matter.

CGR: mean crop growth rate.

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CONCLUSIONS

To determine what possible impact of changes in leaf canopy has had on enhancing wheat yield, crosses were made between two erect and two droopy leaf parents. The resulting progenies were advanced to F6 generations where a high level of homozygosity was achieved. A significant feature of the F6 derived lines was the common genetic background they were derived from; thus making comparisons between leaf types more meaningful.

Based on the results from two experiments, the following conclusions were drawn: i) in both experiments, sharp differences between erect and droopy leaf parents for canopy architectural traits, components of yield, and grain yield disappeared as the F6:2 lines became intermediate between parents, ii) in the first experiment where comparisons were made on contrasting groups of random F6:2 lines derived from four crosses, no consistent direct beneficial effects of erect leaf canopy on grain yield were observed when the whole F6:2 were compared, *iii)* the differences between erect and droopy leaf lines emerged when F6:2 lines involving individual parents were considered, iv) some parents had more impact on their progeny performance of one leaf type than the other, v) positive complementary relationships among grain yield, harvest index, grains/m^2, and 100 kernel weight played an important role in enhancing grain yield of F6:2 lines, regardless of leaf types, vi) F6:2 lines involving specific parents showed a higher susceptibility to leaf tip burning, and this susceptibility affected grain yield through 100 kernel weight.

In the second experiment where comparisons were made between contrasting paired F6:2 lines, vii) erect leaf did show slight beneficial effects on grain yield, viii) radiation absorbed was lower in erect leaf F6:2 lines but no differences in efficiency of converting solar radiation into dry matter was detected, ix) no consistent differences between the two canopy types were observed for extinction coefficient, x) erect leaf counterpart accumulated more dry matter and had higher crop growth rate, xi) the differences in grain yield were independent of efficiency of converting solar radiation into dry matter, crop growth rate, or extinction coefficients, but rather dependent on grains/m^2, harvest index, and leaf duration.

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